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Using Ant Communities for Rapid Assessment of Terrestrial Ecosystem Health

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Abstract

Ecosystem health with its near infinite number of variables is difficult to measure, and there are many opinions as to which variables are most important, most easily measured, and most robust, Bioassessment avoids the controversy of choosing which physical and chemical parameters to measure because it uses responses of a community of organisms that integrate all aspects of the system in question. A variety of bioassessment methods have been successfully applied to aquatic ecosystems using fish and macroinvertebrate communities. Terrestrial biotic index methods are less developed than those for aquatic systems and we are seeking to address this problem here.

This study had as its objective to examine the baseline differences in ant communities at different seral stages from clear cut back to mature pine plantation as a precursor to developing a bioassessment protocol. Comparative sampling was conducted at four seral stages; clearcut, 5 year, 15 year and mature pine plantation stands. Soil and vegetation data were collected at each site. All ants collected were preserved in 70% ethyl alcohol and identified to genus.

Analysis of the ant data indicates that ants respond strongly to the habitat changes that accompany ecological succession in managed pine forests and that individual genera as well as ant community structure can be used as an indicator of successional change. Ants exhibited relatively high diversity in both early and mature seral stages. High ant diversity in the mature seral stages was likely related to conditions on the forest floor which favored litter dwelling and cool climate specialists.

Key Words

ants
invertebrates
pine plantation
rapid bioassessment
seral stage

Introduction

The concept of "ecosystem health" is currently being debated (Calow 2000; Nielsen 1999; Rapport 1999; Suter 1993; Wicklum and Davies 1995; and others) as to its meaningfulness and applicability; however, we are using it here as shorthand for a complex group of related ecosystem concepts. This concept is important because it can provide information about effects of various external influences such as invasive species and chemical, nuclear, and physical disturbance. Ecosystem health is also treated as a measure of the rate or trajectory of degradation or recovery of systems that are currently suffering impact or those where restoration or remediation has taken place. Further, ecosystem health is the single best indicator of the quality of long term environmental stewardship because it not only provides a baseline condition, but also the means for future comparison and evaluation. Ecosystem health is difficult to measure because there are a multitude of biotic and abiotic variables and no consensus as to which suites of variables are truly indicative of ecosystem condition. It would be impossible and prohibitively expensive to measure all those variables, or even just the ones that were certain to be valid indicators. Measurement of ecosystem health can also be a controversial topic for applied ecologists because there are many opinions as to which variables are the most important, most easily measured, and most robust. One approach that avoids some of the controversy of choosing which physical and chemical parameters to measure is bioassessment which evaluates ecosystem health using responses of organisms within the system itself, thus integrating all aspects of the system in question.

Historically measurements of surrogate parameters such as extensive water chemistry data in aquatic systems have been used in an attempt to quantify anthropogenic change. Unfortunately, pollution is frequently transient and the effects are often missed when only traditional chemical and physical water quality monitoring methods are used. On the other hand, communities of organisms living in such bodies of water integrate pollutant effects over time and may show effects at low levels of chronic disturbance. Thus for aquatic systems, especially streams, a number of investigators have successfully applied bioassessment protocols of various sorts (Karr 1991; Clarke 1993; Rossaro and Pietrangelo 1993; Growns et al. 1997; Thorne and Williams 1997; Guérold 2000; Paller et al. 2005; etc.). One protocol for assessing environmental stress came to be accepted in the 1980's when the Index of Biotic Integrity (IBI) was developed (Karr et al. 1986). This system collects an array of fish community metrics within a stream ecosystem and develops a score or rating for the relative health of the ecosystem. The IBI, though originally developed for Midwestern streams, has been successfully adapted to other ecoregions and taxa (macroivertebrates, Lombard and Goldstein, 2004) and has become an important tool for scientists and regulatory agencies alike in determining the health of stream ecosystems. The IBI is a specific type within the larger group of rapid bioassessment (RBA) tools. These protocols have the advantage of directly measuring responses of the organisms affected by system perturbations, thus providing an integrated evaluation of system health because the organisms themselves integrate all aspects of their environment and its condition. In addition to the IBI, the RBA concept has also been applied, with varying success, to other ecosystems like slope wetlands (Paller et al. 2005) and terrestrial systems (O'Connell et al. 1998, Kremen et al. 1993, Rodriguez et al. 1998, Rosenberg et al. 1986). Terrestrial bioassessment methods have lagged somewhat behind those for aquatic systems because terrestrial systems are less distinctly defined and seem to have a less universal distribution of an all-inclusive taxon, such as fish in the IBI, upon which to base an RBA.

In the last decade, primarily in Australia, extensive development of an RBA using ant communities has shown great promise. Ants have the same advantage for terrestrial RBAs that fish do for aquatic systems in that they are an essential and ubiquitous component of virtually all terrestrial ecosystems.

They occupy a broad range of niches, functional groups, and trophic levels and they possess one very important characteristic that makes them ideal for RBA because, similar to the fishes, there is a wide range of tolerance to conditions within the larger taxa. Within ant communities there are certain groups, genera, or species that may be very robust and abundant under even the harshest impacts. There are also taxa that are very sensitive to disturbance and change and their presence or absence is also indicative of the local conditions. As with the aquatic RBAs using feeding groups of macroinvertebrates, ants have a wide variety of functional groups (Table 1), by whose abundance or scarcity an evaluation of the system health may be made (Andersen et al., 2004). Much of the ground work has been done for useful ant RBAs, but it has primarily been in Australia, Europe, the United States desert Southwest, and South America (Australia; Majer and Nichols, 1998, Andersen, 1990, Read, 1996, Lobry de Bruyn, 1999, Majer et al. 1984, Majer 1985, Anderson, 1997, Oliver and Beattie, 1996: Europe; Puszkar, 1978, Gomez et al. 2003: South America; Bestelmeyer and Weins, 1996, Majer, 1992, Kalif et al. 2001, Osborn et al. 1999, Estrada M. and Fernandez C. 1999: Southwestern United States and Mexico; Kaspari and Majer, 2000). A significant amount of success has been shown by these studies in evaluating restoration and recovery from a variety of different anthropogenic impacts. The existing work and body of knowledge has transported well to other ecoregions and as has been done with the IBI, it could be adapted to use in the Southeastern United States. Although some preliminary work has been done in North America (Andersen, 1997), few studies have applied the concept to the U.S. Southeast (Graham et al. 2004a and b), but none has been done in the sense of developing a regional adaptation of Andersen's (1990) original concept as was done by Paller et al. (1996) with the Index of Biotic Integrity (IBI, Karr 1991). It would be necessary to allocate the local ant fauna to functional groups, and evaluate metrics and characteristics to develop indices. Successful adaptation and application of an ant RBA would provide a cost effective, useful, and robust tool for evaluating the health of terrestrial ecosystems anywhere in the region.

Methods and Materials

Study Site

Because our objective was to develop a community baseline by comparing ant communities in different seral stages of pine plantations, sampling was conducted at 4 sites, all located close to each other . A 200 meter transect with sample points at 10 meter intervals was established at each site and GPS coordinates were taken at the ends of each transect (Figure 1). While we sampled across four different seral stages we kept soil type as uniform as possible because ground dwelling ants are profoundly affected by soil structure. The four seral stages sampled were clearcut, 5 year, 15 year and mature planted pine stands. All transects were linear except the 15 year where proximity of hardwood habitat necessitated it being a "T" shape. Rogers (1990) describes the characteristics of the soil types at these locations, and all are siliceous sand with loamy or fine-loamy components.

Each of the pine plantation sampling sites was analyzed for vegetation characteristics. At each sample point the vegetation, litter layer and surface soil characteristics were described. If there was an overstory, the crown closure percentage was estimated, plant species present listed, and the species and diameter at breast height (DBH) of the individual tree nearest the pitfall center were recorded.

The understory layer percent cover was estimated for each sample point. Understory was defined as individual trees or bushes greater than 2 meters in height but less than 5 meters. All data on percent cover were indicated on a ranking from 0 to 6, with 0 being no cover and 6 being 90-100 percent cover. Species that were part of the understory were listed and general comments about the structure were noted. The percent cover of the shrub layer was also estimated, and included woody individuals greater than 1 meter in height. Species in the shrub layer were also listed and general comments noted.

The ground cover percent was estimated for all herbaceous and vine species, species listed, and comments noted. Additionally, this layer was further characterized by distributing the total cover between herb, grass, and vine components using 10 percent increments.

Each sample point was divided into quadrants to sample litter depth and soil organic components. A sample point approximately 1 meter from the pitfall trap was established in each quadrant and the depth of the litter layer recorded and the composition of the litter noted. At the same point, the depth or presence of organic matter in the soil profile was measure and recorded. This was a measure of root penetration as well as organic migration from the litter. The four points at each pitfall location were averaged to provide data for the sample location.

Sampling Procedures

Delabie et al. (2000) and Bestelmeyer et al. (2000) have extensively compared and evaluated the numerous types of sampling methods for capturing ants. The culmination of this work led to the development of the ALL (Ants of the Leaf Litter) protocol (Agosti and Alonso 2000) as a standard method for collecting ants for rapid bioassessment. The ALL protocol uses a 200 meter transect with sample stations at 10 meter intervals, providing 20 sample locations. Sweep net sampling was added to the ALL protocol in order to assess the ants on the low vegetation as well as those on the ground and in the litter. Pitfall trap and sweep net sampling was conducted at each sample point; meter square litter samples were taken at each odd-numbered sample points. Pitfall traps were "double cupped" and allowed to stand for 6 days to account for the "digging in" effect (Greenslade 1973). After this period the traps were set by removing the inner cup and placing in the remaining cup 50 to 75 ml of a mixture of 70% ethyl alcohol and propylene glycol, traps were then allowed to collect for 3 days. Sweep netting of grass and foliage was conducted for one minute at each sample point after which ants were removed from the nets and preserved in 70% ethyl alcohol. Litter samples were collected and placed directly into Winkler bag funnels with chemical heat packs and hung in the field for 3 days. Ants from these samples were then preserved in 70% ethyl alcohol and stored. Invertebrates were picked from the samples under a binocular dissecting microscope and

placed in fresh 70% ethyl alcohol. Only ants were retained for identification from litter and sweepnet samples. All invertebrates from the pitfall traps were retained and identified to major taxon, while ants were separated for identification to genus.

Specimen Identifications

Originally ants were to be identified to genus using identification keys from Bolton (1994); however, using these keys was found to be time consuming because of the large number of genera in the keys that do not occur in this geographical area. To make this process less time consuming a list of genera was arrived at for the Savannah River Site by using Van Pelt and Gentry (1985), and then adding Florida genera from Deyrup (2003) and Deyrup et al. (1989) and Georgia genera from Graham et al. (2004b) and Ipser et al (2004). A new set of identification keys was developed using this list of genera and, where possible, anatomical traits that are easy for non-specialists to identify were used. The following sources were used to identify characters and couplets that could be used to make a rapid identification key: Graham et al. (2004a); McGown (date uncertain); Plowes and Patrock (2000), Van Pelt and Gentry (1985); and Mackay and Mackay (date uncertain). This set of keys (Martin, unpublished) is posted at http://www.osti.gov/servlets/purl/893100-WhBUwA/.

Statistical Analysis

Nonmetric multidimensional scaling (NMS), a relatively assumption free ordination method, was used to identify patterns among samples based on ant genera data. Three NMS ordinations were generated. Each was repeated with different random starting configurations to obtain a final solution with consistent and low stress (i.e., distortion between similarity rankings and distance rankings in the ordination plot). The number of significant dimensions (axes) in each NMS was determined by a Monte Carlo procedure that compared the stress in the ordinations with the stress in randomized data arrangements (McCune and Mefford 1999). The first ordination was based on a Bray-Curtis similarity matrix of the ant genera presence/absence data at each sample station as indicated by all sampling methods combined. Spearman correlation coefficients (rs) were used to

assess the influence of habitat variables on the axes produced by this ordination. The second NMS ordination was based on a matrix of the number of ant genera in each function group at each sampling station, also based on all sampling methods combined. The third NMS ordination consisted of a comparative meta-analysis based on a matrix of presence/absence pitfall data from our four pine plantation transects combined with presence absence data from pitfall traps deployed at Fort Benning, Georgia (Graham et al. 2004b) and northern Florida (Lubertazzi and Tschinkel 2003).

Because each seral stage was subsampled with a number of individual plots, it was possible to construct species accumulation curves and estimate the total number of ant genera in each seral stage with a first-order jackknife estimator (Palmer 1990, McCune and Mefford 1999). Such estimators are useful because the number of species in a sample area is generally greater than the number of observed species.

Results

Habitat differed markedly across the four seral stages under study (Table 2). Overstory and understory canopy cover were much higher in the mature and 15 year transects (28-50% coverage) than in the clearcut and 5 year transects (0-3% coverage) (Table 2). Litter depth was also substantially greater in the 15 year and mature transects (2-4cm) than in the earlier seral stages (1cm). Shrub cover showed the opposite pattern, being higher in the clearcut and 5 year transects (16-43%) than in the 15 year and mature transects (5-6%). Similarly, grass cover was higher in the clear cut and five years transects (4-5%) than in the 15 year and mature transects (<1%).

The number of samples for all sampling methods combined that contained each ant genus is reported in Table 3. If only those genera that were captured 25 or more times are considered, three genera (*Brachymyrmex*, *Solenopsis* and *Dorymyrmex*) were primarily captured in the clearcut transect and in the 5 year transect; three genera (*Crematogaster*, *Paratrechina* and *Aphaenogaster*)

were primarily captured in the 15 year transect and in the mature transect while *Formica* was captured fairly evenly in all transects.

The number of pitfall trap samples that contained each genus is reported in Table 4. If only those genera that were captured 15 or more times are considered, two genera (*Solenopsis* and *Dorymyrmex*) were taken primarily in the clearcut transect and the 5 year transect; two genera (*Crematogaster* and *Aphaenogaster*) were primarily taken in the 15 year transect and in the mature transect while *Formica* and *Paratrechina* were captured in all transects.

The number of litter samples that contained each genus is reported in Table 5. If only those genera that were captured 10 or more times are considered, no genera were primarily caught in the Clearcut transect and the 5 year transect, three genera (*Crematogaster*, *Paratrechina*, and *Aphaenogaster*) were primarily taken in the 15 year transect and in the Mature transect while *Solenopsis* was taken in all transects and *Hypoponera* was taken in all but the 15 year transect.

The number of stations for sweepnet samples that contained each genus is reported in Table 6. If only those genera that were captured 10 or more times are considered, three genera (*Brachymyrmex*, *Solenopsis*, and *Dorymyrmex*) were primarily taken in the Clearcut transect and in the 5 year transect, two genera (*Crematogaster* and *Aphaenogaster*) were primarily taken in the 15 year transect and in the Mature transect while *Camponotus* was taken in all transects

In our study, ants of the genus *Aphaenogaster* occurred at most mature pine stations, most 15 year stations, and three Clear-cut stations; the three Clear-cut stations were the ones having the most residual litter. Zettler et al. (2004) state that *Aphaenogaster* ants nest in litter and organic debris.

We found that *Dorymyrmex* was especially abundant in the five-year recovery transect and less abundant in the clear-cut transect (our most extremely affected); in contrast, at Fort Benning, Georgia, this genus was most abundant and numerically dominant in the most highly disturbed sites (Graham et al. 2004b).

The number of ant genera estimated from the combined pitfall, litter, and sweepnet samples was highest in the clearcut and mature seral stages (17.5 and 17.8, respectively) lowest in the 5 year seral stage (11.8) and intermediate in the 15 year seral stage (13.7) (Figure 2). Pitfall samples alone captured most of the taxa collected by all three methods combined in the clearcut and 5 year transects but were somewhat less effective in the 15 year and mature transects (Tables 3 and 4). Litter samples exhibited the opposite pattern with greater effectiveness in the mature and 15 year transects than the clearcut and 5 year transects (Tables 3 and 5). Sweepnets were effective in the clearcut and 5 year transects but collected only a minority of the genera in the 15 year and mature transects (Tables 3 and 6). These comparisons suggest that a minimum of pitfall and litter samples were needed to adequately represent ant taxa richness across all seral stages, and sweepnet sampling were a useful adjunct sampling method in early seral stages.

Ordination of ant presence/absence data from all sampling sites with a combination of pitfall, litter and sweepnet samples produced two significant ($P<0.05$) axes (Figure 3). The first axis largely separated mature and 15 year sites (with positive scores) from five year and clearcut sites (with negative scores). Litter depth, overstory canopy cover, and understory canopy cover were positively correlated ($rs=0.63$-0.75) and shrub cover was negatively correlated ($rs=-0.71$) with the first axis suggesting that ant community structure responded to habitat changes along the seral gradient represented by the study transects. Several ant genera were largely confined to late seral stage transects including *Aphaenogaster*, a litter nesting genus; *Temnothorax*, a cold climate specialist, and *Crematogaster*, a general Myrmicinae. In contrast, *Dorymyrmex* was restricted to clearcut and 5 year transects. The second axis of the ant MDS was not associated with seral stage nor was it correlated with any habitat variables measured in this study. Two genera, *Paratrechina* and *Hypoponera*, were strongly partitioned along this axis for reasons that cannot be determined with the data we collected. The generalized Myrmicinae genus *Solenopsis* was not included in the ordination because it was present at all sample sites.

The number of ant genera in each functional group (Table 2) was used as the basis of a second ordination to obtain additional insights into the distribution of ants among the study transects. This MDS produced two significant ($P<0.05$) axes and, like the ordination of the ant presence/absence data, separated older (mature and 15 year) and younger (clearcut and 5 year) seral stages on axis 1 (Figure 4). This separation was associated with greater numbers of opportunist and cold climate genera in the older seral stages and an absence of hot climate specialists in some of the older seral stage sample sites. This distribution of climate specialists follows expectations since overhead canopy cover likely maintained lower ground and near-ground level temperatures in the older seral stage transects. Axis 2 was correlated with the number of cryptic and specialized predator genera for reasons that are unclear at this time.

Figure 5 is a graphic representation of the ordination of our data combined with that of Graham et al. (2004b) and Lubertazzi and Tschinkel (2003) and based on presence or absence of specific genera of ants. The Florida and Fort Benning, Georgia sites are distinctly separated on MDS axis 1 reflecting the influence of geography on ant community structure. Several genera including *Odontomachus*, *Cyphomyrmex*, *Neivamyrmex*, and *Pyramica* were collected only from Florida. In contrast, *Prenolepis* was collected only from Georgia, and *Dorymyrmex* was collected primarily from South Carolina and Georgia. To a lesser degree, Axis 1 also separated sites on the basis of disturbance. The Fort Benning data had sites with low and medium levels of disturbance clustering together while the three highly disturbed sites were separate. These patterns suggest that disturbance may produce some community changes that parallel those associated with geographic trends.. A remaining pattern shown by the ordination is that differences in community structure were much greater among the South Carolina sites than among the Georgia or Florida sites, likely because several seral stages were sampled in South Carolina compared with only one in Florida and Georgia.

Discussion

Before changes in insect communities can be generalized to vascular plant community changes or stress in vertebrate communities, linkage among the communities must be verified. Our data suggested that vegetation related differences associated with seral stage strongly affected ant community structure. However, patterns seen in vascular plant communities and in vertebrate communities often do not match well when compared with patterns noted in invertebrate communities For example, in an Austrian study, characterization of a site based on plant community differed significantly from the characterization based on ant communities (Englisch et al. 2005). This is thought to be because the distribution of terrestrial invertebrates is more finely patterned than is the case for either vertebrates or vascular plants and this makes finding surrogates for invertebrate distribution patterns difficult (Abensperg-Traun et al. 1996; Andersen et al. 2004).

Also, what humans see as environmental stress may not be stress to insects. In a European study, hay meadows, meadows, pastures, and silage meadows examined using ant communities showed no differences among treatments; the only factors that appeared to influence ant communities were soil moisture and soil nitrogen (Dahms et al. 2005). It may be that because of low grazing pressure (1.5 cow hectare^{-1}) and frequency of mowing (1 to 3 times per year), the disturbance levels were similar among treatments. Bestelmeyer and Wiens (2001) found that in semiarid areas of the American Southwest livestock grazing that has very noticeable effects on plant communities has little effect on ant community structure and, for some ant species, the few noticeable changes may be the result of soil compaction.

Given that there may be only poor correlation between terrestrial invertebrate communities and vascular plant or vertebrate communities, is it legitimate to worry about assessing terrestrial arthropod community structure and not the whole ecosystem? Aside from the economic impacts of agricultural and forest pests and their predators and parasites, in many geographical areas arthropods are important soil formers and soil fertility mediators (Lobry De Bruyn and Conacher 1990; Farji Brener and Silva 1995; Knoepp et all 2000; etc.). In addition ants are known to be very important food sources for vertebrates that society does value. Ants of the genera *Camponotus* and *Formica* may at times make up 97% of pileated woodpecker diet (Bull et al. 1992) while arboreal

ants of the genus *Crematogaster* are the dominant food item in the diet of the red cockaded woodpecker (Hess and James 1998), a species of concern in the Southeast.

In those cases where invertebrate communities and vascular plant communities are reacting similarly, can stress on ecosystems be measured using ant communities? The answer is an equivocal yes. At Fort Benning, Georgia, disturbance by military maneuvers resulted in significant changes in the ground-foraging ant communities while producing no measurable effect on the ants living or foraging on trees (Graham et al. 2004b). A complicating factor is that species richness of ant communities tends to be higher under moderate disturbance than under either high disturbance or low disturbance regimes (Abensperg-Traun et al. 1996). Under some circumstances ants can be even used as indicators of particular chemical pollution; Hoffmann et al. (2000) reported that ant communities were clearly affected in two habitat types by medium and high dry deposition of SO_2 In that study, ant functional group information provided no additional information about stress levels.

In a study of ants in longleaf pine stands with varying amounts of herbaceous and woody understory that were being managed to return them to the "native" longleaf pine-wire grass ecosystem, there were significant negative correlations between both ant diversity and ant species evenness with increasing herbaceous ground cover (primarily wire grass) (Lubertazzi and Tschinkel 2003); this study reported four species that were more abundant with higher herbaceous ground cover, the "natural condition" of longleaf pine savannas, while ten other species decreased in abundance under the same circumstances.

In one South Carolina study, ant diversity declined significantly for 24 months following clear-cutting (Zettler et al. 2004); despite overall loss in species numbers two species of *Pheidole* and the red imported fire ant (*Solenopsis invicta*) rapidly colonized the clear-cut areas and were abundant through the two years of the study. These species are socially dominant and appear to reduce the ability of other species to colonize near them.

In our study, richness of ant genera was lowest in the transect where there had been five years recovery; this pattern is different from that noted by Punttila et al. (1991) in Finland. Witford and Gentry (1981) reported higher ant diversity in recently planted longleaf pine plantation than in mature, thinned or recently burned stands. Lough (2003) reported higher densities and diversities of ants in "older clearcuts" where canopy closure had not yet occurred and ant diversity was similar between new clearcuts and mature plantations.

Analysis of our data indicates that ants respond strongly to the habitat changes that accompany ecological succession in managed pine forests and that individual genera as well as ant community structure can be used as an indicator of successional change. Ants exhibited relatively high diversity in both early and mature seral stages. High ant diversity in the mature seral stages was likely related to conditions on the forest floor which favored litter dwelling and cool climate specialists. In the mature pine stand litter layers were thicker than in other stands and probably provide more insulation thus equilibrating temperature while reducing soil moisture loss through evaporation.

Some of our analyses were based on functional groups. Functional groups are used in analyses of these sorts in an attempt to reduce apparent complexity in communities and to identify general patterns of community structure across biogeographical boundaries (Andersen 1997). Functional groups also tell us important ecological facts about the ant community with which we may be working. One of these facts is the community resistance to invasion by nonindigenous species and persistence of species in the presence of such invasions. The presence of socially dominant forms, such as *Iridomyrmex* spp. in Australia, appear to make an area less susceptible to invasion by nonindigenous species; other guilds or functional groups that persist in the presence of nonindigenous invasive species are the hypogaeic (cryptic) ants and the ants that specialize in either cold climate or hot climate (Holway et al. 2002). North American ant faunas are depauperate in dominant Dolichorinae and it appears that their function in North America might be filled by genera in the "generalized Myrmicinae" category (Andersen 1997). While some "generalized Myrmicinae" genera such as *Pheidole* and *Solenopsis* have species that are socially dominant in longleaf pine

habitat, it appears that their influence may be limited to short distances from their nests (Lubertazzi and Tschinkel 2003).

Some functional groups also add significantly to community predictability across wider geographic areas. Arboreal ants are, on average, twice as resistant to desiccation as ground-foraging ants (Hood and Tschinkel 1990) and for this reason the arboreal ant communities of north Florida pines are remarkably consistent across pine habitats (Lubertazzi and Tschinkel 2003). Additionally, Graham et al. (2004b) reported that arboreal ant communities were also remarkably similar between oak and pine trees in the same habitats. Hypogaeic (cryptic) ant communities in longleaf pine flatwoods, because they forage in an area having restricted ranges in humidity and temperature, appear to be consistent across a wide geographic area (Lubertazzi and Tschinkel 2003).

In general, members of a particular functional group tend to react similarly to any given form of stress. Hoffmann and Andersen (2003) list some stresses that tend to solicit reactions from particular functional groups. Cryptic species tend to respond to all perturbances that influence litter layer integrity. In Australia, opportunists often proliferate in the presence of disturbance unless there is a dominant dolichoderine to hold them in check while, in forested areas, fire or grazing disturbances tend to favor increases in dominant dolichoderines and hot climate specialists. On the other hand, buildup of litter in forested areas seems to favors opportunists and reduces abundance of dominant dolichoderines and hot climate specialists. In wetter forests, clear cuts and extensive wildfires leads to proliferation of opportunists. Generalized Myrmicines and opportunists tend to have opposite reactions to disturbance while specialized predators are usually too rare and infrequently captured for them to indicate much of anything.

There are some methodological caveats that we must address. Identification to lower taxonomic levels (family-, genus- or species-level) is most suitable for biological monitoring (Basset et al. 2004; Guérold 2000; etc.) while sorting only to higher taxonomic levels appears to be better suited for studies at broader geographic scales (Basset et al. 2004; Hewlett 2000). We are uncertain at this

stage how wide of a geographical area our findings apply to but we think that subfamily- and genus-level identification is sufficiently fine scale for our goal of rapid assessment.

The question of appropriate taxonomic level for an analysis is often raised, especially where morphospecies are used. Morphospecies are taxa where there may be multiple taxa included but all individuals are fundamentally similar. Oliver and Beattie (1996a, 1996b) found that when analysis was done using morphospecies of ants, beetles and spiders and the analyses were done again using species identified by experts, the results were fundamentally the same. Analyses using morphospecies of different guilds performed better at distinguishing among habitats than did analyses using morphospecies all belonging to the same guild, so that including more taxa in an analysis does not ensure that a data set will have greater discriminatory power (Basset et al. 2004). We feel that we addressed this problem by using as many functional groups of ants as were available. In a study by Schnell et al (2003) identification to either morphospecies or to genus level was sufficient to use ant community composition to differentiate among 6-year old eucalypt plantation, pasture and naturally regenerating woodland and to distinguish between newly planted eucalypt plantation and 6 years of growth.

Figure 5 show there is a lot more variability in the ant faunas of our four sites than occurred in the studies by Graham et al. (2004b) or Lubertazzi and Tschinkel (2003). We believe that the reason for this is that we examined four different seral stages while the other studies were all within a single sere. There is some support to this hypothesis in that our mature pine transect is more similar to the Fort Benning and Florida stations than it is to any of our other sites and, in the ordination based on functional groups, the 15 year site is much nearer to these other sites than are either the clearcut or the 5 year sites. If other data supports this hypothesis then it would appear that seral stages should be considered when an RBA is developed using ant faunas in forested locations.

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Table 1. Ant functional groups as used in this study.

Functional Group	Definition
dominant Dolichoderinae	refers to behavioral dominance over other forms at bait stations
subordinate Camponotini	refers to behavioral dominance at bait stations in the absence of "dominant Dolichoderinae"
hot climate specialists	genera specialized to live in hot, xeric habitats
cold climate specialists	genera specialized to live in cold or temperate areas
tropical climate specialists	genera having distributions centered in the tropics
cryptic species	forms that are seldom seen because they are small and subterranean (hypogaeic)
opportunists	forms that have wide geographical ranges and generalized foraging
generalized Myrmicinae	Myrmicinae that are behaviorally competitive but not necessarily dominant
specialist predators	forms that are specialized for capturing particular prey items*
arboreal	forms that are specialized to nest and forage in trees or bushes
social parasite	forms that either are slave raiders or are inquilines (live in other species' nests)
invasive	species that have been introduced and often become abundant or problematical

*Andersen (2004) restricts "specialist predators" to some larger Ponerinae that avoid competing with the “dominant Dolichoderinae” by foraging on prey not readily taken by that functional group. We include some species that are small and cryptic but forage on a very limited number of forms (e.g. *Myrmecina* specializes in hunting mites).

Table 2. Average percent cover (standard deviation) in the four habitats under study

Cover type	Clearcut	5 year	15 year	Mature
Overstory cover (%)	0(0)	0(0)	50(25)	46(19)
Understory cover (%)	0(0)	3(3)	28(19)	29(19)
Shrub cover (%)	16(16)	43(18)	4(5)	6(6)
Total groundcover (%)	14(13)	13(5)	13(15)	19(21)
Herbaceous groundcover (%)	2(2)	2(1)	0(1)	2(2)
Grass groundcover (%)	5(8)	4(3)	0(1)	1(2)
Vine groundcover (%)	7(9)	7(4)	13(14)	16(18)
Litter depth (cm)	1(1)	1(0)	2(1)	3(1)
Soil depth (cm)	2(1)	2(0)	2(0)	3(1)

Table 3. Frequency of capture of the genera of ants using pitfall, litter, and sweepnet data combined. The 15 year category is based on a total of 48 samples while the others have 50 samples each.

Subfamily	Genus	Functional Group	Clearcut	5 Year	15 Year	Mature
Myrmicinae	*Cephalotes*	arboreal	2	0	0	0
Pseudomyrmicinae	*Pseudomyrmex*	arboreal	0	0	6	0
Formicinae	*Camponotus*	Camponotus	3	8	4	9
Myrmicinae	*Temnothorax*	cold climate specialist	1	0	10	8
Formicinae	*Acanthomyops*	cryptic species	1	0	0	0
Formicinae	*Brachymyrmex*	cryptic species	8	14	0	3
Myrmicinae	*Pyramica*	cryptic species	0	0	0	1
Myrmicinae	*Strumigenys*	cryptic species	0	0	0	2
Myrmicinae	*Crematogaster*	generalized Myrmicinae	2	0	21	20
Myrmicinae	*Pheidole*	generalized Myrmicinae	1	1	7	2
Myrmicinae	*Pogonomyrmex*	hot climate specialist	0	4	0	0
Myrmicinae	*Solenopsis*	hot climate specialist	34	39	14	14
Dolichoderinae	*Dorymyrmex*	opportunists	14	30	1	0
Dolichoderinae	*Forelius*	opportunists	0	2	0	2
Dolichoderinae	*Tapinoma*	opportunists	0	2	1	0
Dolichoderinae	*Technomyrmex*	opportunists	10	4	1	1
Formicinae	*Formica*	opportunists	5	13	10	9
Formicinae	*Paratrechina*	opportunists	5	8	13	14
Myrmicinae	*Aphaenogaster*	opportunists	9	1	17	36
Myrmicinae	*Tetramorium*	opportunists	0	2	0	1
Myrmicinae	*Monomorium*	social parasite	0	1	0	0
Myrmicinae	*Myrmecina*	specialized predator	1	0	6	6
Ponerinae	*Amblyopone*	specialized predator	0	0	0	1
Ponerinae	*Hypoponera*	specialized predator	6	4	0	6
Myrmicinae	*Cardiocondyla*	tropical climate specialist	0	0	1	0
Myrmicinae	*Trachymyrmex*	tropical climate specialists	0	0	1	4

Table 4. Frequency of capture of the genera of ants using pitfall data only. The 15 year category is based on a total of 19 samples while the others have 20 samples each.

Subfamily	Genus	Functional Group	Clearcut	5 Year	15 Year	Mature
Myrmicinae	*Cephalotes*	arboreal	1	0	0	0
Formicinae	*Camponotus*	Camponotus	0	2	2	7
Myrmicinae	*Temnothorax*	cold climate specialist	1	0	2	4
Formicinae	*Brachymyrmex*	cryptic species	2	6	0	3
Myrmicinae	*Strumigenys*	cryptic species	0	0	0	2
Myrmicinae	*Crematogaster*	generalized Myrmicinae	0	0	11	8
Myrmicinae	*Pheidole*	generalized Myrmicinae	1	0	6	0
Myrmicinae	*Pogonomyrmex*	hot climate specialist	0	4	0	0
Myrmicinae	*Solenopsis*	hot climate specialist	20	20	10	9
Dolichoderinae	*Dorymyrmex*	opportunists	8	19	0	0
Dolichoderinae	*Forelius*	opportunists	0	2	0	1
Dolichoderinae	*Tapinoma*	opportunists	0	1	0	0
Dolichoderinae	*Technomyrmex*	opportunists	5	4	0	0
Formicinae	*Formica*	opportunists	4	11	6	7
Fromicinae	*Paratrechina*	opportunists	2	5	5	5
Myrmicinae	*Aphaenogaster*	opportunists	5	1	9	10
Myrmicinae	*Tetramorium*	opportunists	0	2	0	0
Myrmicinae	*Myrmecina*	specialized predator	0	0	4	0
Ponerinae	*Amblyopone*	specialized predator	0	0	0	1
Ponerinae	*Hypoponera*	specialized predator	3	1	0	1
Myrmicinae	*Cardiocondyla*	tropical climate specialist	0	0	1	0
Myrmicinae	*Trachymyrmex*	tropical climate specialist	0	0	0	0

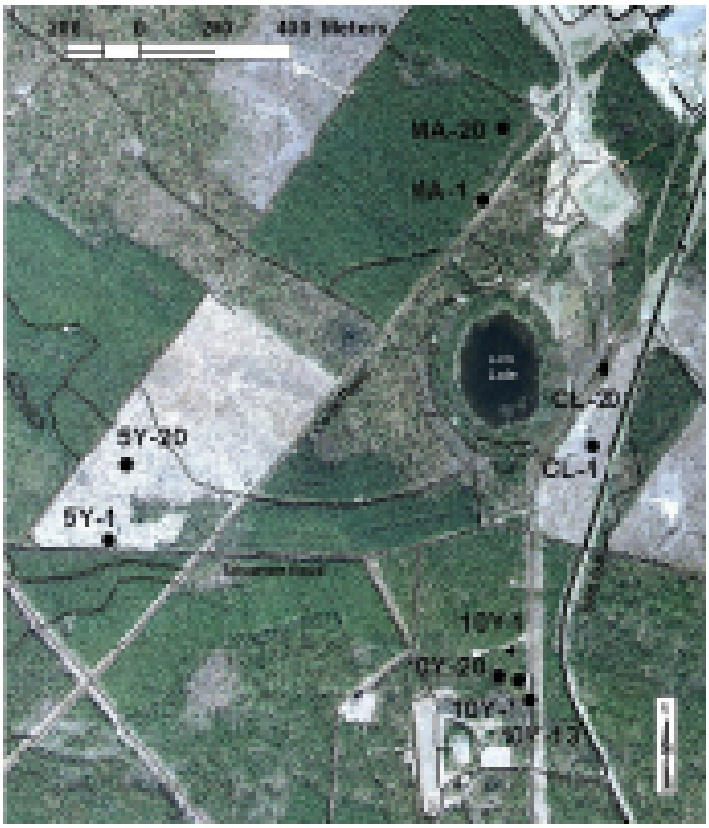
Table 5. Frequency of capture of the genera of ants using litter data only. All transects have 10 samples each.

Subfamily	Genus	Functional Group	Clearcut	5 Year	15 Year	Mature
Myrmicinae	*Cephalotes*	arboreal	1	0	0	0
Formicinae	*Camponotus*	Camponotus	0	3	0	0
Myrmicinae	*Temnothorax*	cold climate specialist	0	0	1	3
Formicinae	*Brachymyrmex*	cryptic species	1	0	0	0
Myrmicinae	*Pyramica*	cryptic species	0	0	0	1
Myrmicinae	*Crematogaster*	generalized Myrmicinae	0	0	5	6
Myrmicinae	*Pheidole*	generalized Myrmicinae	0	0	1	2
Myrmicinae	*Solenopsis*	hot climate specialists	5	6	4	4
Dolichoderinae	*Dorymyrmex*	opportunists	0	2	0	0
Dolichoderinae	*Forelius*	opportunists	0	0	0	1
Dolichoderinae	*Tapinoma*	opportunists	0	0	1	0
Dolichoderinae	*Technomyrmex*	opportunists	0	0	1	0
Formicinae	*Formica*	opportunists	0	1	1	0
Formicinae	*Paratrechina*	opportunists	2	2	7	8
Myrmicinae	*Aphaenogaster*	opportunists	4	0	5	9
Myrmicinae	*Tetramorium*	opportunists	0	0	0	1
Myrmicinae	*Myrmecina*	specialized predator	1	0	2	6
Ponerinae	*Hypoponera*	specialized predator	3	3	0	5
Myrmicinae	*Trachymyrmex*	tropical climate specialists	0	0	1	4

Table 6. Frequency of capture of the genera of ants using sweepnet data only. The 15 year category is based on a total of 19 samples while the others have 20 samples each.

Subfamily	Genus	Functional Group	Clearcut	5 Year	15 Year	Mature
Pseudomyrmicinae	*Pseudomyrmex*	arboreal	0	0	6	0
Formicinae	*Camponotus*	Camponotus	3	3	2	2
Myrmicinae	*Temnothorax*	cold climate specialist	0	0	7	1
Formicinae	*Acanthomyops*	cryptic species	1	0	0	0
Formicinae	*Brachymyrmex*	cryptic species	5	8	0	0
Myrmicinae	*Crematogaster*	generalized Myrmicinae	2	0	5	6
Myrmicinae	*Pheidole*	generalized Myrmicinae	0	1	0	0
Myrmicinae	*Solenopsis*	hot climate specialist	9	13	0	0
Dolichderinae	*Dorymyrmex*	opportunist	6	9	1	0
Dolichoderinae	*Tapinoma*	opportunist	0	1	0	0
Dolichoderinae	*Technomyrmex*	opportunist	5	0	0	1
Formicinae	*Formica*	opportunist	1	1	3	2
Formicinae	*Paratrechina*	opportunist	1	1	1	1
Myrmicinae	*Aphaenogaster*	opportunist	0	0	3	17
Myrmicinae	*Monomorium*	social parasite	0	1	0	0

Figure 1. Locations of sampling areas in relationship to each other and to significant local surface features.



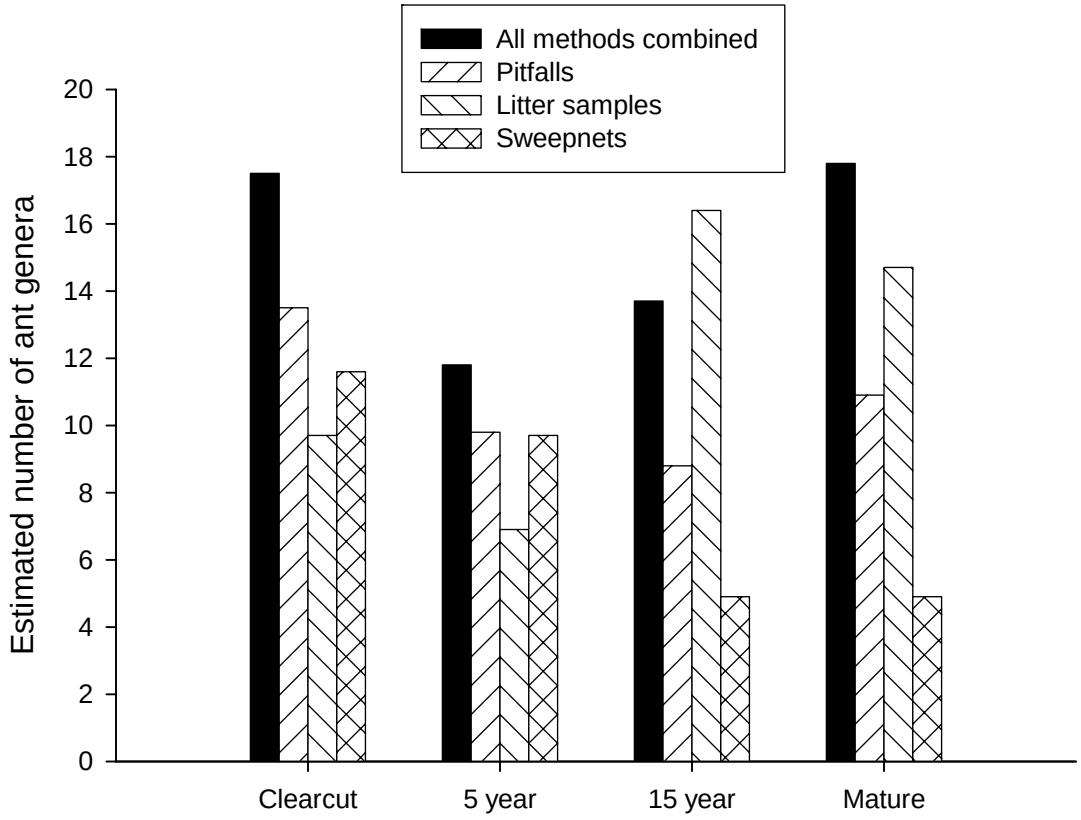


Figure 2. Estimated number of ant genera in four seral stages in managed pine forests in South Carolina.

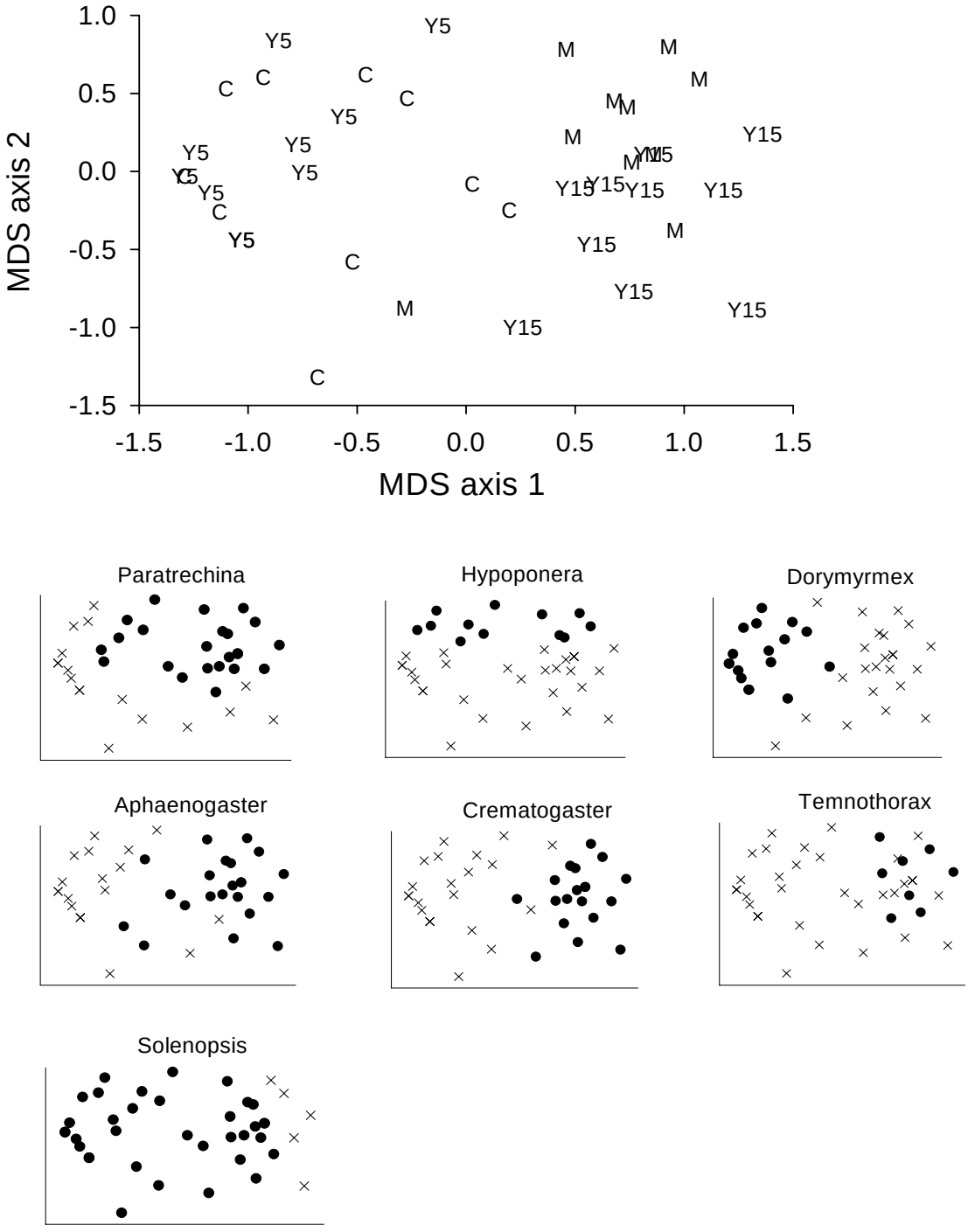


Figure 3. Ordination (nonmetric multidimensional scaling) of the sample sites based on the presence/absence of ant genera collected in pitfall, litter, and sweepnet samples. Clearcut (C), 5

year (Y5), 15 year (Y15), and Mature (M) seral stages are shown. Presence is indicated by a dot and absence by an X.

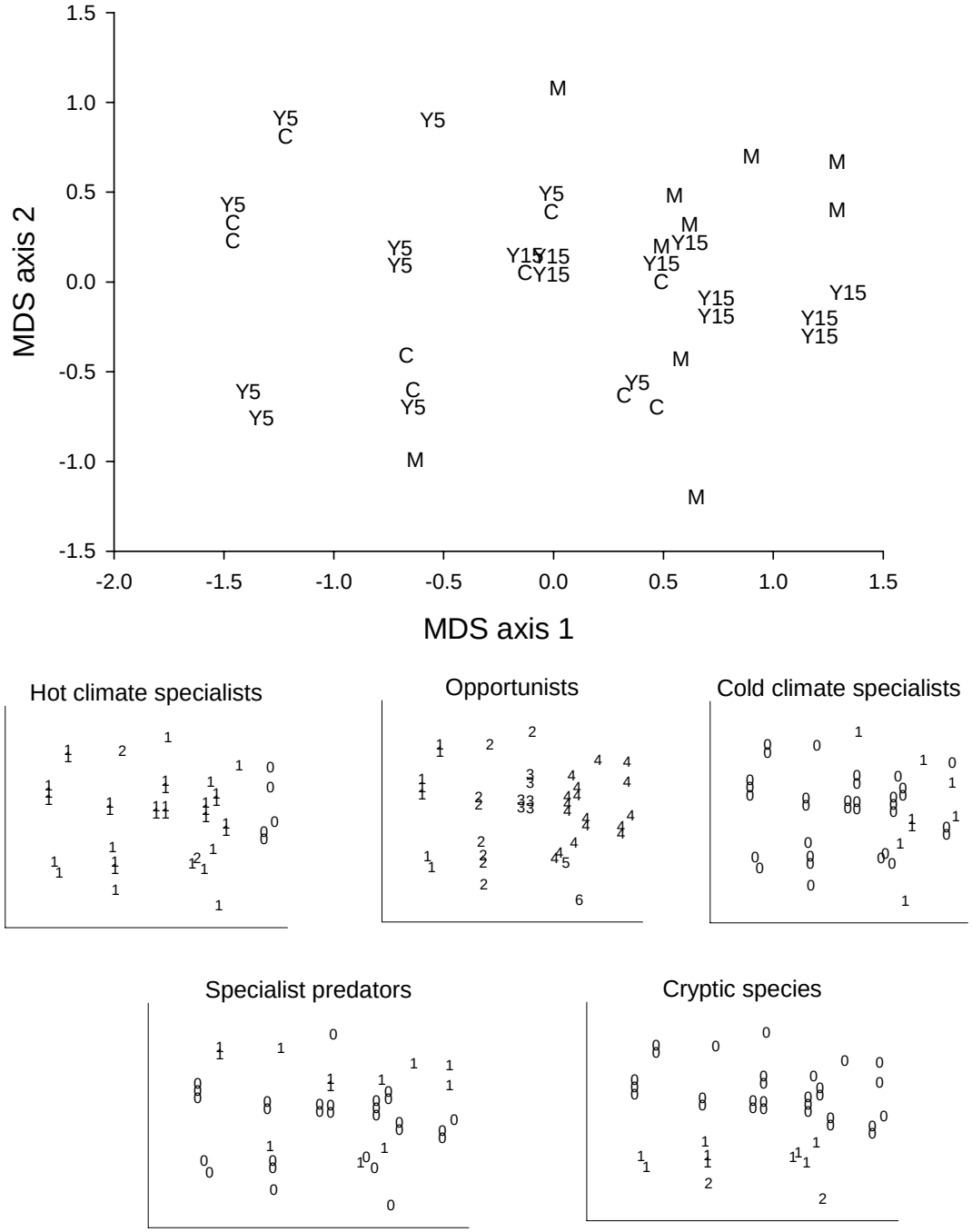


Figure 4. Ordination (nonmetric multidimensional scaling) of the sample sites based on the number of ant genera in each ant functional group. Clearcut (C), 5 year (Y5), 15 year (Y15), and Mature (M) seral stages are shown.

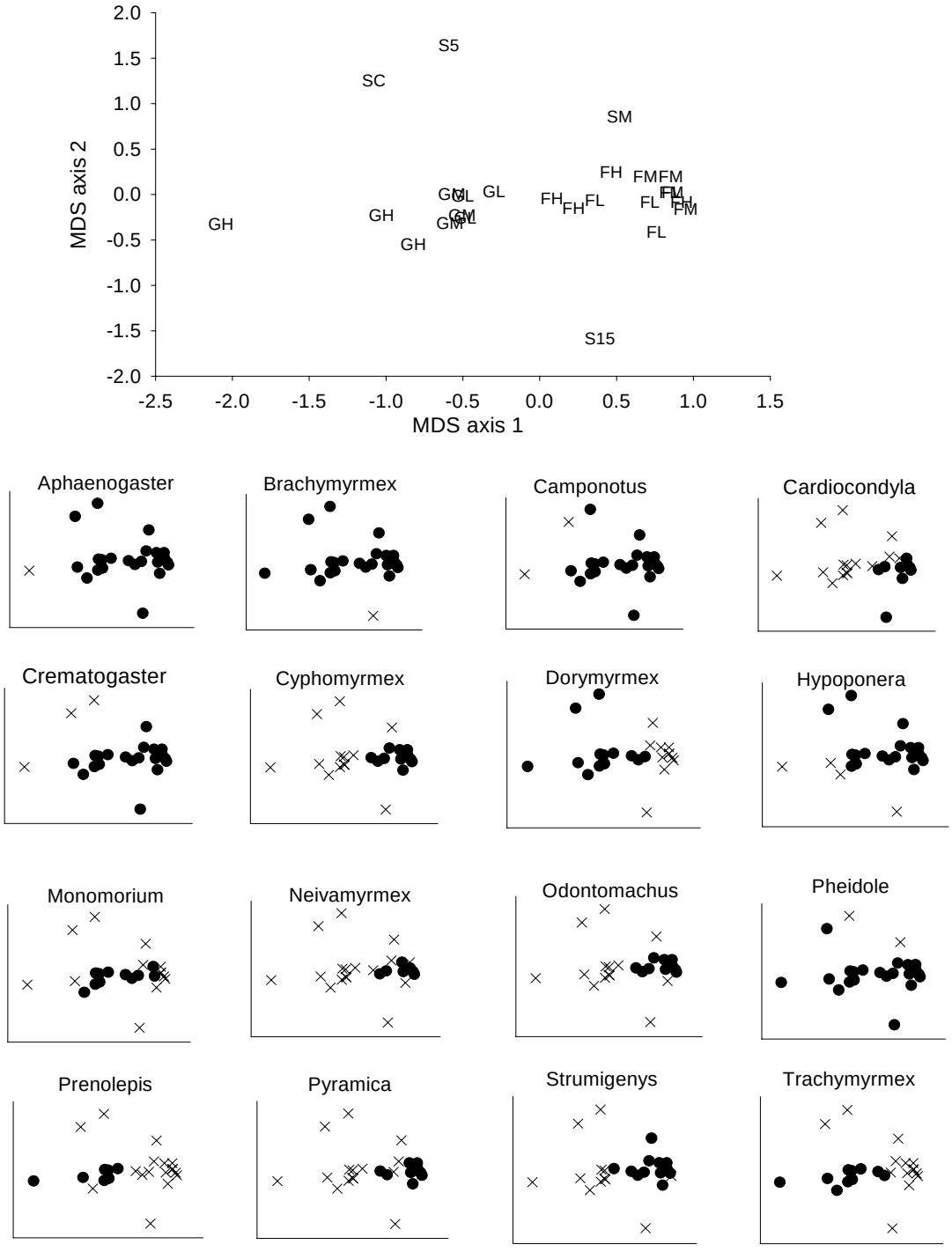


Figure 5. Ordination (nonmetric multidimensional scaling) of sample sites in South Carolina, Georgia (Graham et al., 2004) and Florida (Lubertazzi and Tschinkel 2003) based on presence/absence of ant genera at each site. Sample sites in Florida (F) and Georgia (G) differed in disturbance level

(H=high, M=medium, L=low). Sample sites in South Carolina (S) were in clearcuts (C), mature pine forests (M) or in intermediate seral stages (5 years and 15 years after clearcutting). The presence (dot) and absence (X) of individual ant genera is also shown.